

Developmental Age and Taxonomic Affinity of the Mojokerto Child, Java, Indonesia

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ABSTRACT An increasing number of claims place hominids outside Africa and deep in Southeast Asia at about the same time that *Homo erectus* first appears in Africa. The most complete of the early specimens is the partial child's calvaria from Mojokerto (Perning I), Java, Indonesia. Discovered in 1936, the child has been assigned to *Australopithecus* and multiple species of *Homo*, including *H. modjokertensis*, and given developmental ages ranging from 1–8 years. This study systematically assesses Mojokerto relative to modern human and fossil hominid growth series and relative to adult fossil hominids.

Cranial base and vault comparisons between Mojokerto and *H. sapiens sapiens* (*Hss*) ($n = 56$), Neandertal ($n = 4$), and *H. erectus* ($n = 4$) juveniles suggest a developmental age range between 4 and 6 years. This range is based in part on new standards for assessing the relative development of the glenoid fossa. Regression analyses of vault arcs and chords indicate that *H. erectus* juveniles have more rounded frontals and less angulated occipitals than their adult counterparts, whereas *Hss* juveniles do not show these differences relative to adults. The growth of the cranial superstructures and face appear critical to creating differences in vault contours between *H. erectus* and *Hss*.

In comparison with adult *H. erectus* and early *Homo* ($n = 27$) and adult *Hss* ($n = 179$), the Mojokerto child is best considered a juvenile *H. erectus* on the basis of synapomorphies of the cranial vault, particularly a metopic eminence and occipital torus, as well as a suite of characters that describe but do not define *H. erectus*, including obelion depression, supratotal gutter, postorbital constriction, mastoid fissure, lack of sphenoid contribution to glenoid fossa, and length and breadth ratios of the temporomandibular joint. Mojokerto is similar to other juvenile *H. erectus* in the degree of development of its cranial superstructures and its vault contours relative to adult Indonesian specimens. The synapomorphies which Mojokerto shares with *H. erectus* are often considered autapomorphies of Asian *H. erectus* and confirm the early establishment and long-term continuity of the Asian *H. erectus* bauplan. This continuity does not, however, necessarily reflect on the pattern of origin of modern humans in the region. *Am J Phys Anthropol* 102:497–514, 1997.

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An increasing number of claims place hominids outside Africa and deep in Southeast Asia at about the same time that *Homo erectus* first appears in Africa (1.8 million years ago) (Swisher et al., 1994; Gabunia and Vekua, 1995; Huang et al., 1995). If

these early Asian dates are correct, the first hominids to leave Africa could have been a species of early *Homo* or an australopithe-

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cine. Because of this, the morphological attributes of these early extra-African hominids are of renewed interest. Yet each of the early specimens represents challenges to taxonomic classification (e.g., Huang et al., 1995; Schwartz and Tattersall, 1996; Bräuer and Schultz, 1996; Etler et al., submitted).

The most complete of the early specimens is the child's calvaria from Mojokerto¹ (Perning I), Java, Indonesia (Figs. 1, 2). The child is significant because it represents the earliest evidence of hominids in island Southeast Asia at 1.81 mya (Swisher et al., 1994). However, the fragmentary nature of the specimen complicates the determination of developmental age, which has been suggested to be as little as 1 year to greater than 8 years (Dubois, 1936; Koenigswald, 1936; Weinert, 1938; Grimm, 1940; Weidenreich, 1940a; Storm, 1994; Antón, 1995). And Mojokerto's youth complicates the determination of taxonomic affinity, which has been suggested to be with *Australopithecus* and various species of *Homo*, including *Homo modjokertensis* (Dubois, 1936; Koenigswald, 1936; Weinert, 1938; Grimm, 1940; Weidenreich, 1940a; Storm, 1994; Antón, 1995; Campbell, 1973; Jacob, 1975; Sartono, 1975; Clark, 1978).

To date the specimen's developmental age and specific hominid classification remains contentious (Howell, 1994). Shortly after its discovery, Koenigswald (1936) used Mojokerto as the type specimen of *Homo modjokertensis*. However, neither his original nor subsequent descriptions compare Mojokerto with more than a few juvenile specimens nor differentiate the child sufficiently from *H. erectus* (Koenigswald, 1936, 1940). Koenigswald considered Mojokerto between 2 and 5 years old, while Weidenreich (1940a), who also used the name *H. modjokertensis*, considered the child to be about 18 months old. Weidenreich's (unpublished) notes at the American Museum of Natural History for the paper he intended to devote to Mojokerto reveal that the basis for his estimates of

developmental age were three modern children's crania. Despite using the name *H. modjokertensis*, both Weidenreich and Koenigswald considered Mojokerto a juvenile *Pithecanthropus erectus* (Koenigswald and Weidenreich, 1939). Koenigswald (1975) later rescinded this statement.

Other authors reached different conclusions. Dubois (1936) recognized no Pithecanthropine or unique traits in Mojokerto and sank *H. modjokertensis* into *H. soloensis*. Grimm (1940) argued for the morphological reality of *H. modjokertensis* on the basis of differences between the midorbital sagittal profiles of Mojokerto and adult Indonesian *P. erectus*. However, his argument is not compelling since lateral facial structures (e.g., midorbital structures) develop later than midsagittal structures and thus should differ between juveniles and adults of the same species (e.g., Antón, 1994). Also on the basis of sagittal profiles and brain size, Weinert (1938) favored an association between Mojokerto and *H. sapiens* but settled for referring the specimen to *Homo sp.* due to its great geological age. Using a single comparative juvenile, each of these studies reached different developmental age estimates for Mojokerto. These estimates affected projections of adult brain size that in turn influenced the taxonomic associations favored by each author. However, the relative strength of the different age estimates cannot be assessed without reference to a human growth series encompassing a range of individual variation.

More recent overviews that do not exclude the child place Mojokerto in *H. erectus* by default (e.g., Risçutia, 1975; Clark, 1978; Howells, 1980; Sartono, 1981). Some recognize Mojokerto as *Pithecanthropus modjokertensis* (Jacob, 1975; Sartono, 1975), one of three species that are, however, more parsimoniously included within *H. erectus* (*sensu* Weidenreich, 1940b; Clark, 1978; de Vos et al., 1994). Others sink *H. modjokertensis* into *Australopithecus* (Campbell, 1973), although there is no other compelling argument to recognize *Australopithecus* in Asia (Kramer, 1994).

Only two recent studies have considered the affinities and/or age of the Mojokerto child explicitly (Storm, 1994; Antón, 1995).

¹The current spelling of the region is *Mojokerto*. The Indonesian language has undergone revision by removing all the *ds* preceding *js*. The species name because of the law of priority of zoological nomenclature remains *modjokertensis*, with a *d*. To correlate with regional maps, recent spelling is used in all but the species designation.

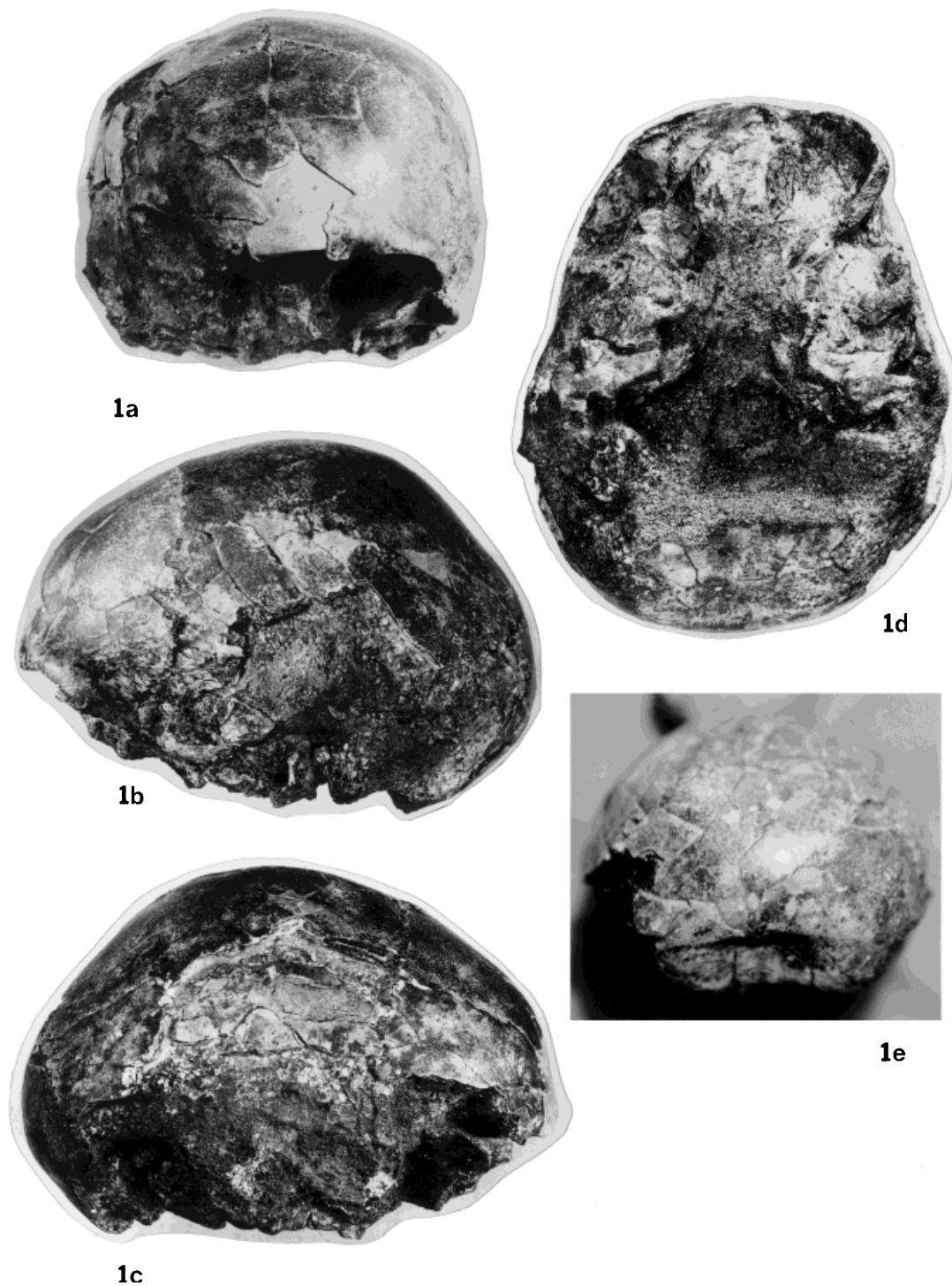


Fig. 1. Mojokerto (Perning I). Photos 1a–d from Weidenreich (unpublished) archive, AMNH, courtesy Department of Library Services, AMNH; copies by J. Beckett. Photos precede application of pigment to matrix. Photo 1e courtesy Dr. C.C. Swisher III. **a:** Frontal view (neg. 2A22933). **b:** Left lateral (neg. 2A22934). Note supratatorial sulcus, obelion depression. **c:** Right lateral (neg. 2A22935). Note obelion depression. **d:**

Basal view (neg. 2A22936). Note the well-developed continuous articular eminence extending most of length of fossa. Note medial-lateral expansion of fossa. The large swellings posterior to both petrous pyramids are shaped pumice, not mastoid processes. **e:** Occipital view. Note development of occipital torus. For scale, parietal chord is 86.4 mm.



Fig. 2. Superior view of cast of Mojokerto (Perning 1). Note supratatorial sulcus on left. Photo courtesy Dr. C.C. Swisher III. For scale, parietal chord is 86.4 mm.

Storm concludes Mojokerto is a juvenile *H. erectus* by comparing the anatomy of Mojokerto to the definitions of *H. erectus*, *P. robustus*, and *P. modjokertensis*. He does not compare the specimen directly to a range of fossil *H. erectus* or to non-Asian hominids. Although Storm carefully outlines the general factors, such as age, sex, and pathological conditions, that influence skull morphology, he is unable to refine an age determination by comparison to modern human or fossil hominid growth series due to a lack of comparative material (Storm, personal communication).

This paper extends my previous work by providing a systematic evaluation of the developmental age and taxonomic affinities of the Mojokerto specimen relative to a large comparative sample of fossil and modern hominids (Table 1). My primary objective is to account for the affects of immaturity on the expression of taxonomically salient characters in Mojokerto. Subsequently, I test the null hypothesis that Mojokerto is a member of *H. erectus* (*sensu stricto*) by scoring the appearance and form of morphological traits considered synapomorphic or autapomorphic for *H. erectus* (Table 2) relative to *H. habilis sensu lato* and *Hss* specimens. Al-

TABLE 1. Sample sizes and sources of hominid cranial material

Sample	N	Origin of metrics ¹
Subadults		
<i>Homo sapiens</i>	56	
Unknown	52	Antón (UOP)
Australia	4	Antón (AMNH)
Neandertals		
Devil's Tower 1, Pech de l'Aze, La Quina 18, Teshik Tash	4	Morphological only
<i>Homo erectus</i>		
Ngandong 2, KNM-WT 15000, Zhoukoudian Skull III, Skull VIII	4	Antón
Early <i>Homo</i> —OH 7, 13, 16	3	Wood, 1991
Adults		
<i>Homo sapiens</i>	179	
Australia—multiple	47	Antón (AMNH, UOP)
Coobol Creek	29	Brown, 1989
Fossil <i>Hss</i> —Wajak 1, Kow Swamp 5, Nacurrie 1 and 2, Keilor	5	Brown, 1989; Jacob, 1967
Papua New Guinea	89	Hambly, 1940
Modern Caucasian	9	Antón (UF)
<i>Homo erectus</i>	22	
Sangiran 2, 3, 4	3	Antón
OH-9, KNM-ER 3733, 3883, Sangiran 10, 12, 17	6	Wood, 1991
Trinil, Ngandong 1, 4, 5, 6, 8, 9, 10, 11; Zhoukoudian II, X, XI, XII	13	Santa Luca, 1980
Early <i>Homo</i>		
OH-24, KNM-ER 1813, 1805, 1470, 3732	5	Wood, 1991

¹ Morphological comparisons made by Antón on original and cast material as noted in text. AMNH, American Museum of Natural History; UF, University of Florida; UOP, University of the Pacific. Other abbreviations as per text.

though I favor the inclusion of Ngandong within *H. erectus*, I evaluated the Mojokerto child relative to the most conservative definitions of *H. erectus*: those based on the early Southeast Asian material. Primary metric data for Mojokerto are available in Koenigswald (1936, 1940) and will not be repeated here.

MATERIALS AND METHODS

Materials

The Mojokerto specimen was recovered in 1936 from a tuffaceous conglomeratic sandstone of the Kedoengwaroe anticline near Perning, East Java (Koenigswald, 1936, 1940; Terra, 1943). Because controversy soon arose surrounding the exact provenience of

TABLE 2. Distribution of cranial characters in Mojokerto and other fossil hominids

Characters ¹	Mojokerto	<i>H. habilis</i>	<i>H. erectus</i>	Ngandong	<i>Hss</i>
Occipital torus	+	0	+	+	0
Metopic eminence	+	0	+	+	0
Bregmatic eminence	0	0	+	+	0
Sagittal keel	0	0	+	+	0
Angulated occipital	i	0	+	+	0
Fissure between mastoid-tympanic	+	+	+	+	0
Sphenoid contributes to TMJ	0	0	v	v	+
Recess between entoglenoid-tympanic	+	0 ²	+	+	v
Obelion depression	+	0	+	+	0
Postorbital constriction	s	s	s	w	w
Supratoral gutter	+	0	+	+	0
Anteroposteriorly broad TMJ	+	0	+	+	+
Strong articular eminence	+	0	+	+	+
Weak postglenoid process	+	0	+	+	+
Cranial capacity (in cc)	740–860 (adult)	500–750	750–1059	1013–1251	—

¹ First five characters are synapomorphies for *H. erectus*. +, present; 0, absent; i, incipient; s, strong; v, variable; w, weak. *H. erectus* exclusive of Ngandong. *Hss*, *Homo sapiens sapiens*. See text for sample composition, trait definition, and cranial capacity citations.

² Tobias (1991) distinguishes the morphology of the medial glenoid fossa in *H. habilis* from that in *H. erectus* contra Bräuer and Mbua (1992).

the specimen, mineralogical studies of sediments from the purported excavation pit were conducted in 1938. These studies supported the association between these sediments and those adhering to the specimen (Terra, 1943: p 443). More recent microprobe analysis of minerals removed from within the calvaria and those collected from the purported find section also support their association (Swisher et al., 1994). Nonetheless, the exact find spot remains unknown. It seems clear, however, that the specimen came from a pumice-bearing level in the region of Mojokerto. To date, the pumice level dated by Swisher and colleagues (1994) to 1.81 mya is the *youngest* of these levels known from that section. Mojokerto is thus the earliest hominid known from island Southeast Asia.

The specimen consists of a partial calvaria retaining most of the superior vault and portions of the anterior and middle cranial base (Fig. 1). The calvaria is filled with a pumice-bearing matrix which has been removed only from the orbits and the region of the foramen magnum. The matrix is currently painted with a black pigment that sometimes laps onto the broken edges of the bone obscuring the true thickness of the vault bone. Figure 1a–d from the Weidenreich (unpublished) archive precede application of this pigment. The bone itself has been covered in a high-gloss substance that may be a preservative. The frontal squama and

orbital plates are complete except for the right zygomatic process of the frontal, right squama superior to the temporal line, and the midline frontal at and superior to glabella; glabella is reconstructed (Fig. 1a). An incipient eminence is present along the middle third of the metopic suture site. A supratoral gutter is present on the left side (Figs. 1a,b, 2). The coronal suture is complete, and the bregmatic fontanelle is closed, although a small fragment at bregma is missing postmortem (Fig. 2). The left and right parietals are complete along the midline from bregma to lambda and laterally from the sagittal suture to near the level of the temporal lines; the left parietal is more complete inferiorly than the right (Fig. 1b,c). The right parietal sustained moderate medial crushing postmortem. In sagittal view, a depression is present at and posterior to obelion (Figs. 1b,c). The middle two-thirds of the occipital squama and nuchal plane are complete from lambda to just posterior of the foramen magnum; opisthion is reconstructed (Fig. 1d,e). An occipital torus (swelling) is present at midline, delineated by a shallow fossa below (Fig. 1e). The right occipital squama extends toward asterion, preserving much of the region of the mendo-sal suture. The right lateral corner of the occipital squama is displaced anteriorly and medially into the region of the temporal. Both temporal squamae are missing. On the left, the petrous temporal with external

auditory meatus, glenoid fossa, and portions of the zygomatic process of the temporal are virtually intact (Fig. 1d). The left mastoid process is missing. On the right, only the medial half of the glenoid fossa is preserved. The right petrous temporal lacks its most lateral extension. However, the right mastoid process and the fissure between the mastoid process and the petrous temporal are present (Fig. 1d). The left greater wing of the sphenoid is more complete than the right, retaining the infratemporal fossa surface including part of the sphenotemporal suture, most of the temporal fossa region, and the orbital portion from the zygomatic suture to foramen rotundum and superiorly to the articulation with the frontal (Fig. 1a). The right sphenoid is preserved only in the posterior orbit and a small portion of the infratemporal fossa. The body of the sphenoid is missing ectocranially, although the endocranial surface may be preserved beneath the matrix. The ethmoid is present in both the right and left orbits, as witnessed by complete posterior ethmoid foramina, but the midline ethmoid is absent. Thus, the right posterior orbit (sphenoid and ethmoid) and right temporal are completely separated from the frontal (Fig. 1d). As a result, the right posterior orbit rotated slightly laterally postmortem.

The comparative sample (Table 1) consisted of immature modern human crania ($n = 56$), immature fossil *Homo* (originals of Devil's Tower 1, Pech de l'Aze, Ngandong II, and casts of KNM-WT 15000, La Quina 18, Teshik Tash, Zhoukoudian Skull III, Skull VIII, OH-7, OH-13, and OH-16), adult *H. sapiens* from Australia, Papua New Guinea, and modern Caucasians ($n = 179$), adult *H. erectus* (originals of Sangiran 2, 3, 4, 12, 17, Trinil, casts of the Ngandong and Zhoukoudian series, OH-9, KNM-ER 3733, 3883), and adult early *Homo* (casts OH-24, KNM-ER 1813, 1805, 1470, 3732). I made morphological comparisons on the basis of originals and casts as noted above. Metrics were taken by me and from published sources as noted in Table 1.

Developmental age

Although it would be ideal to assess Mojokerto's developmental age primarily by

comparison with early *Homo* and *H. erectus* juveniles, there are few such fossils, and all are likely to be developmentally older than Mojokerto. Early *Homo* specimens OH-13 and OH-16 are nearly adult, with third molars erupting (Tobias, 1991), and thus of little use in determining Mojokerto's developmental age. OH-7 and KNM-ER 1590 preserve fragments of parietal not useful in determining a developmental age range. Of the four, only OH-13 is complete enough for inclusion in vault contour analysis (see below). Only eight reportedly subadult *H. erectus* specimens preserve areas comparable to Mojokerto: Sangiran 3, Ngandong 2, 5, 8, 9, Zhoukoudian Skull III, Skull VIII, and Skull IX, and KNM-WT 15000. Sangiran 3 and Ngandong 5 and 9 are likely to be young adults and are so considered here (Antón and Franzen, 1996, in press). Zhoukoudian Skull III is either an older juvenile or possibly a young adult and is considered here as a tentative juvenile (Black, 1931; see below). Ngandong 8 and Zhoukoudian Skull IX are too fragmentary to be of use. KNM-WT 15000, Ngandong 2, and Zhoukoudian Skull III provided comparisons between subadult and adult *H. erectus* from the same region, comparisons that were used to evaluate the relationship between Mojokerto and adult *H. erectus* in Indonesia. The Zhoukoudian Skull VIII occipital fragment provides morphological comparisons. The juvenile fossil specimens used here are, from developmentally oldest to youngest, Skull III/OH-13/OH-16, KNM-WT 15000/OH-7?, Ngandong 2/Skull VIII, and Mojokerto.

Because Mojokerto is developmentally the youngest of these fossil juveniles, I also compared it with a range of Neandertal juveniles and a large sample of modern human juveniles. These samples included newborn to 11-year-old modern humans (dental developmental ages [Ubelaker, 1984]) and Neandertals between 1.5 and 8 years (dental and cranial developmental ages; see below). The Mojokerto child's age is expressed here as both a descriptive developmental stage and as dental/cranial developmental age (*sensu* Smith, 1993).

Because Mojokerto lacks dental remains, I focussed on the relationship between relative cranial development and dental develop-

TABLE 3. Development of the tympanic plate and glenoid fossa in Mojokerto and juvenile Neandertals

	Mojo	Pech	Gibraltar	La Quina	Teshik Tash	Modern age/years
Tympanic plate (after Weaver, 1979)						
U-shaped ring (stages 2/3)	0	X	0	0	NA	0.5–2
Central patency (stages 4/5)	0	0	X	0	NA	1.5–2.5
Fused (stage 6)	X	0	0	X	NA	2.4–4
Glenoid fossa						
Shallow cup	0	X	0	0	0	0.5
Articular tubercle	X	X	X	X	X	>2
Continuous eminence	X	0	0	X	X	4–5
Mediolateral elongation	X	0	0	X	X	>4
Adult depth	0	0	0	X	X	>7

¹ NA, area damaged; X, present; 0, absent.

mental ages in the comparative sample. Because similar cranial development in Neandertals and modern humans correlates with somewhat different dental eruption ages in each (e.g., Tillier, 1982; Dean et al., 1986), I discuss the Neandertal sample in terms of both their cranial and dental development. Devil's Tower 1 (Gibraltar 2) is approximately 3–4 years old based on perikymata development (Dean et al., 1986; Stringer et al., 1990). This age is consistent with the development of the temporal region (especially the glenoid fossa) which is similar to that of the 3-year-old modern human sample used here and by Tillier (1982). Although the dental developmental age, based on modern human eruption standards, is between 4 and 5 years, the perikymata suggest dental eruption is accelerated relative to cranial development in Neandertals (Dean et al., 1986). Pech de l'Aze is younger than Devil's Tower 1. The cranial base and vault of Pech de l'Aze suggest an age of 2 or less in comparison with the modern human sample used here (Legoux (1966, 1970) and Patté (1957) assign an age of 2.5 years). Alternatively, dental development suggests an age of 2.5–3.6 years (Minugh-Purvis, 1988). La Quina 18 and Teshik Tash have been assigned dental developmental ages between 6 and 8 and 8 and 12 years, respectively (Martin, 1920; Weidenreich, 1945; Legoux, 1966; Minugh-Purvis, 1988). The acceleration of Neandertal dental development/eruption relative to cranial development may indicate cranial developmental ages of 7 years or less for La Quina 18 and 7–9 years for Teshik Tash.

To assess developmental age in the absence of the face, I compared Mojokerto's

glenoid fossa, petrous, and tympanic portions of the temporal bone, fontanelles, and sutural closure to modern growth standards and fossil hominid juveniles (Table 3). Sutural interdigitation and closure, particularly of the metopic and mendosal sutures, fontanelle closure, and development of the petrous temporal and tympanic vary regularly throughout development (Anderson, 1960; Weaver, 1979; Heim, 1982; Minugh-Purvis, 1988). The form of the articular eminence and glenoid fossa also vary predictably during development, although their pattern of development is not as well documented as for the other features. For this reason, I documented the pattern of development of the glenoid fossa in a modern human growth series (50 specimens between 2 and 11 years dental developmental age) and in fossil juveniles and compared Mojokerto to these standards (Fig. 3; Table 3). Morphological differences between hominine and pongid glenoid fossae (Sherwood, 1995) preclude the use of pongid standards to assess developmental age in Mojokerto. However, dental and other comparisons suggest that *H. erectus* and Neandertal development, while unique, is more similar to human than to pongid patterns (Dean et al., 1986; Bromage and Dean, 1985; Smith, 1993; Tompkins, 1996). Similarly, the prolongation of growth periods typical of modern humans has already begun in early *Homo* (Smith et al., 1995). I did not use endocranial volume to assess developmental age because adult cranial capacities vary significantly among hominid species and the age implied by the volume of the Mojokerto calvaria would vary depending upon the species to which it is assigned.

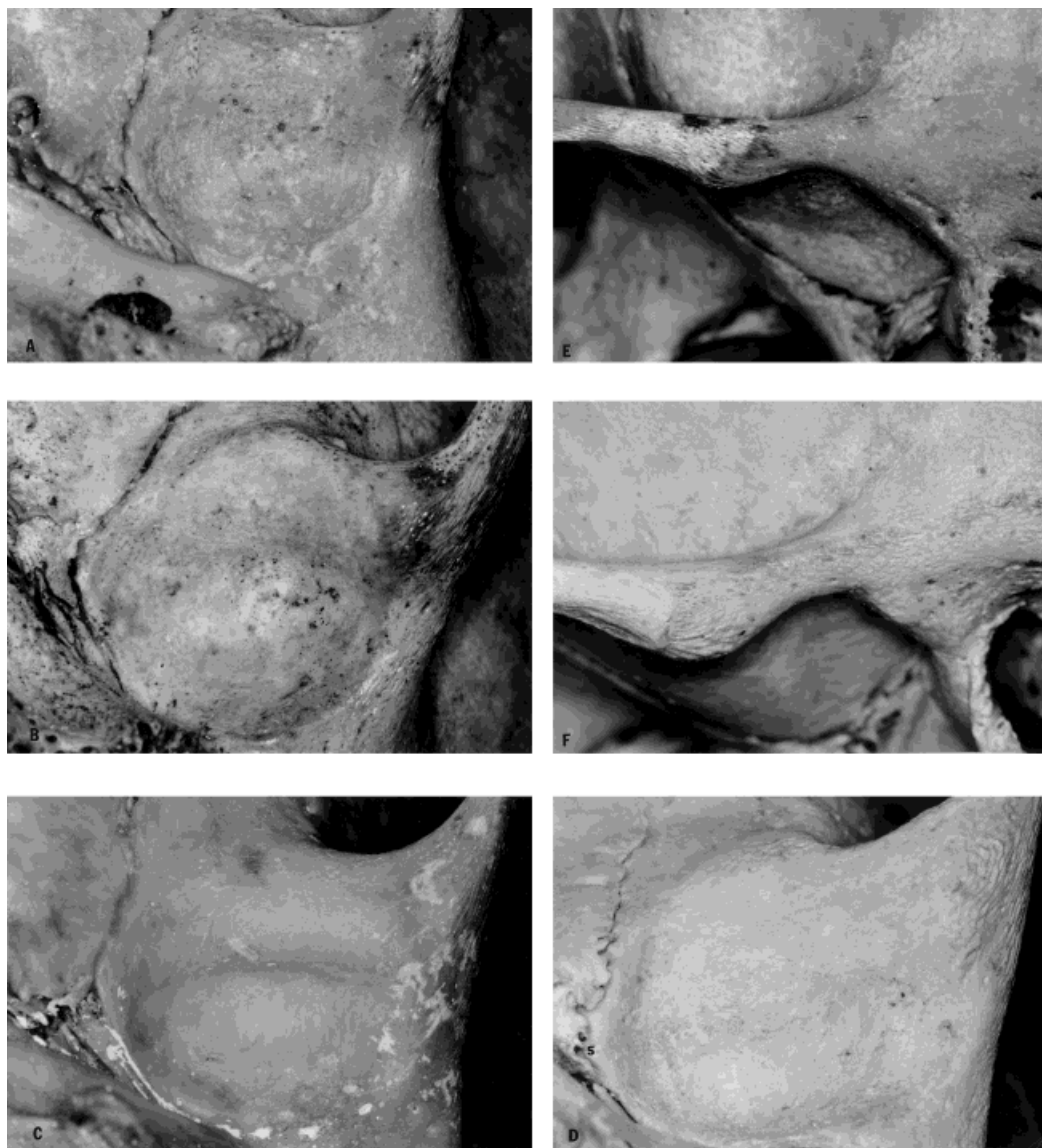


Fig. 3. Glenoid fossa development. Representative examples from modern human growth series ($n = 50$ between ages 2 and 11 years). For A–D, anterior is toward top of page; medial is toward left. Same magnification for A–F. Measurements are provided for scale following each of the individual descriptions. **A:** Two-year-old (SRA: A-75; see E for lateral view). Fossa is shallow, cup-like, and rounded with incipient temporomandibular (articular) tubercle but no continuous articular eminence. Note large central patency in tympanic plate. Glenoid breadth is 16.0 mm, and depth is 3.1 mm. **B:** Four-year-old (SRA: A-89; see F for lateral view). Fossa has enlarged in width, breadth, and depth. The articular eminence is more continuous, bar-like across the front of the fossa. Medial-lateral expansion begins. Central patency of tympanic plate closed. Glenoid breadth is 18.2 mm, and depth is 4.5 mm. **C:** Six-year-

old (SRA: A-96). Fossa is larger and more robust. Articular eminence is more substantial and more complete medially. Postglenoid process is more defined than in B. Glenoid breadth is 19.9 mm, and depth is 3.7 mm. **D:** Eight-year-old (SRA: A-183). Fossa is larger still. Articular eminence now complete in its medial extension. Suture between temporal and sphenoid now complete at its most posterior extent (s; compare with A–C). Glenoid breadth is 20.6, and depth is 5.0 mm. **E:** Two-year-old in lateral view. Anterior is toward the left and superior toward the top of the page. Note shallowness of fossa resulting from lack of articular eminence. **F:** Four-year-old. Orientation as in E. Note increased depth of fossa due to increase in size of articular eminence and temporomandibular (articular) tubercle and beginning definition of postglenoid region.

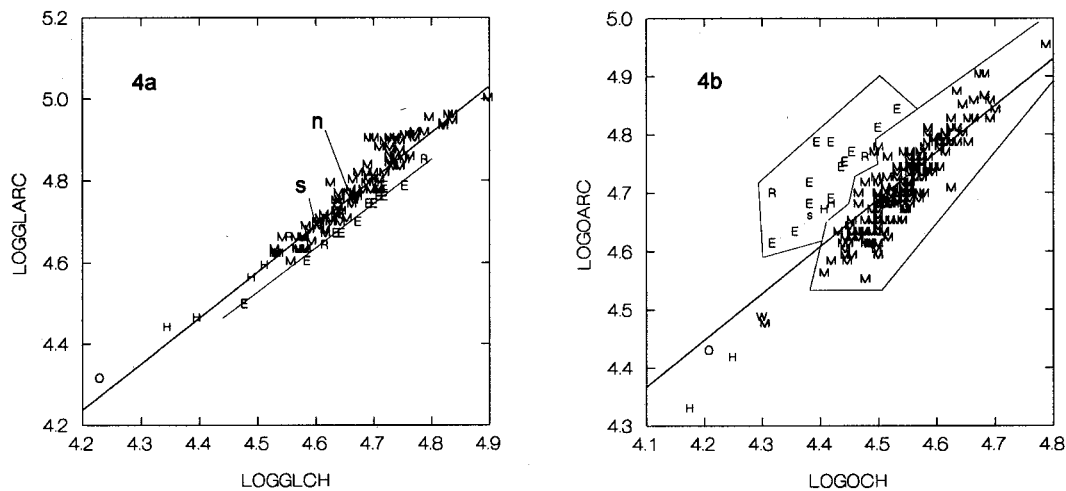


Fig. 4. Log-log plots of frontal and occipital arc vs. chord lengths. E, Asian *H. erectus* including Ngandong; H, *H. habilis*, *sensu lato*; M, modern humans; n, Ngandong II; O, Mojokerto; R, African *H. erectus*; S, Skull III; W, KNM-WT 15000. See Table 4 for regression values calculated separately for M and for R + E samples. Metrics as per Table 1. **a**: Log-log plots frontal arc (LOGGLARC) vs. chord (LOGGLCH). Main line is least-squares regression line for all samples combined. Line through Es represents regression for *H. erectus*. Note

that O, s, and n are all above (more rounded than) the main trend within E. All of the Ngandong adults are amongst the Es below the scatter of *Hss* (= M). **b**: Log-log plots occipital arc (LOGOARC) vs. chord (LOGOCH). Plotted line is least squares regression line for all samples combined. Note that juveniles O and W are less angulated than adult E and R but that older juvenile/young adult s is as angulated as adults. H datapoints near O are OH-24 and OH-13.

Cranial contours and superstructures

Due to its subadult age, it is unlikely that Mojokerto's cranial superstructures are fully developed. I used the slightly older Ngandong 2 and Zhoukoudian Skull VIII specimens as well as KNM-WT 15000 to assess the relative order of development and subadult appearance of these structures.

Sagittal cranial contours differ between early *Homo*, *H. erectus*, and *H. sapiens*, with *H. erectus* having a longer, lower, and more angulated vault than the others (e.g., Howell, 1978; Wood, 1991; Rightmire, 1993). However, in many species sagittal cranial contours also change during development; the frontal becomes less rounded with growth of the face and cranial superstructures and the occipital more angulated with growth of the occipital torus (e.g., Weidenreich, 1940c). It was therefore necessary to evaluate differences in sagittal cranial contours between subadult and adult specimens to consider the relationship of Mojokerto to adult Southeast Asian fossil hominids. Modern human subadults and adults, Ngandong 2 and the adult Ngandong specimens, Zhoukoudian III and adult Zhoukoudian specimens, and

KNM-WT 15000 and adult African *H. erectus* were used for this assessment. Arcs were taken in the sagittal plane with a steel tape placed along the ectocranial surface of each frontal (glabella to bregma), parietal (bregma to lambda), and occipital (lambda to opisthion). Chords were straight-line distances between the same points using Mitutoyo digital sliding calipers. Some comparative metrics are from published sources (Table 1). The relationship between sagittal vault contours was assessed by bivariate plots of log-transformed data of arc vs. chord lengths (Figs. 4, 5; Table 4). Least-squares regressions were calculated by groups, and Tsutakawa and Hewett's (1977) quick test was used to assess differences in y-intercept values (Table 4). *P* values less than 0.01 were considered significant. Given the wide confidence intervals (Table 4), it is unlikely that significant differences would be obtained using different bivariate techniques.

Taxonomic affinity

I assessed Mojokerto's taxonomic affinity by scoring individual cranial vault and base characters relative to Asian and African

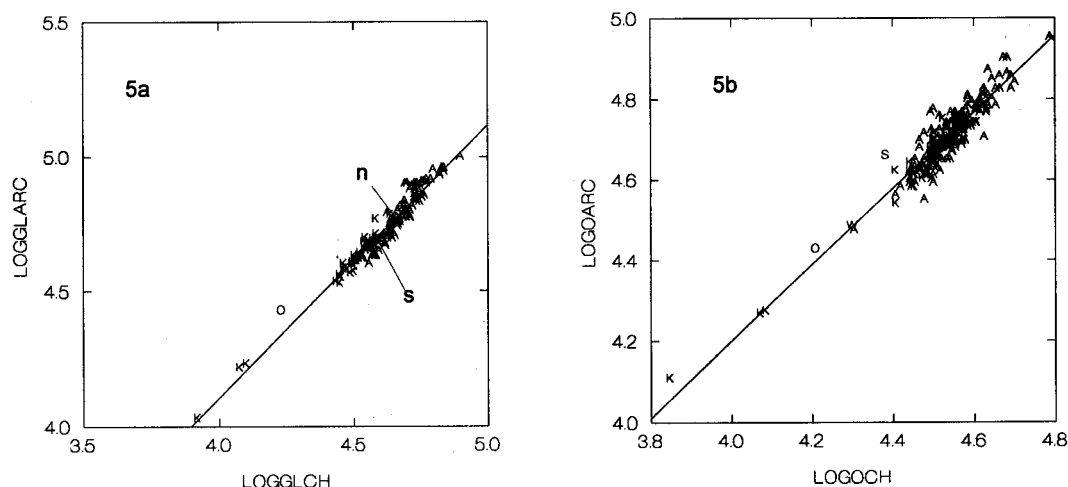


Fig. 5. Log-log plots of frontal and occipital arc vs. chord lengths. A, *Hss* adults; K, *Hss* children; n, Ngandong II; O, Mojokerto; s, Zhoukoudian Skull III; W = KNM-WT 15000. See Table 4 for regression values. Plotted line is combined modern human (A + K) least-squares regression. Metric sources as in Table 1. **a:** Log-log plots frontal arc (LOGGLARC) vs. chord

(LOGGLCH). Note that Mojokerto (O) is slightly above combined regression line and Ngandong II (n) is on that line. **b:** Log-log plots occipital arc (LOGOARC) vs. chord (LOGOCH). Note that both fossil juveniles (O and W) are on combined regression line, whereas older adolescent/young adult Skull III (s) is above the regression line.

TABLE 4. Least squares regression statistics and significance tests for differences between y intercepts¹

	Slope	Y intercept	Standard error	R ²	<i>H. erectus</i> vs. <i>H. sapiens</i> (y intercept)
Frontal arc vs. frontal chord (independent)					
Adult <i>H. erectus</i>	0.97	0.19	0.06	0.94	Smaller
Adult <i>H. sapiens sapiens</i>	1.20	-0.82	0.04	0.90	—
Juvenile <i>H. sapiens sapiens</i>	0.99	0.16	0.02	0.98	—
Combined <i>H. sapiens sapiens</i>	1.01	0.06	0.02	0.95	—
Parietal arc vs. parietal chord (independent)					
Adult <i>H. erectus</i>	0.99	0.11	0.05	0.94	ns
Adult <i>H. sapiens sapiens</i>	1.00	0.09	0.02	0.88	—
Juvenile <i>H. sapiens sapiens</i>	0.93	0.42	0.02	0.97	—
Combined <i>H. sapiens sapiens</i>	0.98	0.19	0.02	0.94	—
Occipital arc vs. occipital chord (independent)					
Adult <i>H. erectus</i>	0.89	0.81	0.16	0.70	Larger
Adult <i>H. sapiens sapiens</i>	1.02	0.08	0.04	0.81	—
Juvenile <i>H. sapiens sapiens</i>	0.90	0.60	0.02	0.96	—
Combined <i>H. sapiens sapiens</i>	0.95	0.38	0.02	0.89	—

¹ ns, not significant, $P > 0.01$; larger, $P < 0.01$ and *H. erectus* larger than *H. sapiens sapiens*; smaller, $P < 0.01$ and *H. erectus* smaller than *H. sapiens sapiens*.

hominids with an emphasis on traits considered syn- or autapomorphic for *H. erectus* (*sensu stricto*) (Table 2). Preservation of the Mojokerto specimen limited character selection. The following characters, considered either synapomorphic or autapomorphic for *H. erectus* by most researchers, were scored: cranial superstructures (metopic eminence, sagittal keel, and bregmatic eminence), occipital torus, and sharp angulation between

the nuchal and squamous portions of the occipital (Delson et al., 1977; Santa Luca, 1980; Stringer 1984, Andrews, 1984; Hublin, 1986; Kennedy, 1991; Li and Etler, 1992; Rightmire, 1993). I also scored characters considered synapomorphic by some (Andrews, 1984; Stringer, 1984; Li and Etler, 1992; Rightmire, 1993) but not all (Hublin, 1986; Kennedy, 1991; Bräuer and Mbua, 1992) researchers: a fissure separating the

mastoid process from the tympanic plate (= mastoid fissure), lack of a sphenoid contribution to the glenoid fossa, and a recess between the entoglenoid pyramid and tympanic. I also assessed the conformation of the temporomandibular joint (TMJ), although it is not clear whether these characters represent derived conditions for *H. erectus* (Table 2) (Picq, 1990). For completeness, I considered characters that are either plesiomorphic or of unclear polarity: obelion depression, sagittal contours, postorbital constriction, and the presence of a supratral gutter (Rightmire, 1993). I did not consider cranial vault thickness because of the youth and preservation of the specimen and the controversy surrounding variability and taxonomic significance of vault thickness (e.g., Smith et al., 1985; Brown, 1994; Hublin, 1986; Kennedy, 1991; Gauld, 1996). Brain size, as estimated following determination of developmental age, was not a direct factor in determining taxonomic affinity. However, I did consider whether this estimate was consistent with the taxonomic designation indicated by the morphological traits.

RESULTS

Developmental age

Sutural and fontanelle closure indicated an age of greater than 2–2.5 years in modern human dental developmental years and greater than 3–4 years (Devil's Tower 1) in Neandertals. The last of the fontanelles closes during the second year of life in modern humans (Ford, 1956; Williams and Warwick, 1986), the mendosal suture begins fusing before birth and is completed between the second and fourth year (Heim, 1982; Minugh-Purvis, 1988), and the metopic suture begins fusing in the second year and is completed by the third year (Minugh-Purvis, 1988). All of the fontanelles are closed in the Mojokerto specimen. The metopic suture is fully fused. The portion of the mendosal suture that is preserved shows no indication of an open suture or fusion scar. However, because the mendosal suture fuses from medial to lateral and the most lateral extent of the occipital is not preserved, it is possible, although unlikely, that the suture's most lateral edge was patent. Fontanelles and sutures are also closed without fusion

scars in the Neandertal sample except Pech de l'Aze; Pech de l'Aze has a patent bregmatic fontanelle and metopic suture (Patté, 1957).

Mojokerto's tympanic plate indicated an age of at least 2.5 years and probably greater than 4 years dental developmental age based on modern human standards and greater than 3–4 years in Neandertals (Devil's Tower 1) (Table 3). In humans, the tympanic portion of the temporal develops from the tympanic ring in a series of well-documented steps (Anderson, 1960; Weaver, 1979; Sullivan and Weaver, 1981; Curran and Weaver, 1982). In its initial stages the ring is patent laterally; that is, the floor and anterior portion of the auditory canal are patent. The ring proceeds to fuse laterally, leaving a central patency in the plate (Fig. 3A) which is usually closed by the dental developmental age of 2.5–4 years in modern humans (Weaver, 1979; Sullivan and Weaver, 1981). Occasionally, the central patency remains in the adult as a tympanic dehiscence (foramen of Huschke [De Stefano and Hauser, 1989]). The tympanic plate of Mojokerto is fully formed without any central patency (Table 3). The tympanic portions of Devil's Tower 1 and Pech de l'Aze are not as well developed as in Mojokerto. Pech de l'Aze maintains an open u-shaped tympanic, whereas Devil's Tower 1 maintains a large central patency. The tympanic is better developed in La Quina 18 than Mojokerto and cannot be assessed in Teshik Tash.

Based on the present skeletal sample, the modern human glenoid fossa develops in a standardized fashion that correlates with dental developmental age (Fig. 3). The fossa starts as a shallow, relatively round cup with a temporomandibular (= articular) tubercle but without an articular eminence. At this early age (6 months) the breadth of the fossa is about one-third of the total distance to the midline of the cranial base; this percentage increases to about 45% in adult humans and is accompanied by increased depth and mediolateral elongation of the fossa and development of an articular eminence. The cup becomes deeper with age and development of the articular eminence. A continuous articular eminence can be seen as early as 3 years in some specimens, but it

is not consistently present until 4–5 years of age (Fig. 3B). Beginning with the 4-year-old sample, some individuals show mediolateral elongation of the fossa. Between the ages of 4 and 6 the human glenoid fossa increases in depth and definition; however, there are no discrete characters which differentiate the 4- from the 6-year-olds in all cases (Fig. 3C). By dental developmental age 7, the articular eminence is sufficiently developed that a 6- and a 7-year-old have demonstrably different patterns. Between 7 years and 11/12 years the fully adult glenoid pattern is developed (Fig. 3D).

The relative development of the glenoid fossa indicates an age of between 4 and 6 years for the Mojokerto child relative to modern human standards (Table 3; Figs. 1d, 3c). During this period the articular eminence is already present as a relatively continuous feature but has not yet reached its adult conformation. Compared to modern humans, the articular eminence in Mojokerto is continuous, although less well-developed medially, and the temporomandibular (articular) tubercle is well developed laterally, corresponding to a developmental age of 5 or 6 years (Fig. 1d). However, the fossa and the articular eminence have not reached their adult conformations, as seen by comparison with adult Indonesian fossils (Sangiran 2 and 17). The glenoid fossa is particularly broad and deep for the overall size of the Mojokerto individual. The glenoid fossa is 46% of half cranial base width, matching the proportions in adult modern humans.

The development of the glenoid fossa of Mojokerto relative to the Neandertal sample supports a developmental age of at least 4 and less than 7 years for Mojokerto. Compared to juvenile Neandertals, the articular eminence of Mojokerto is better developed than Pech de l'Aze and Devil's Tower 1 but less developed than La Quina 18 and Teshik Tash (Table 3). In Mojokerto the eminence is a relatively strong, continuous eminence at the anterior edge of the glenoid fossa. This eminence is absent medially. In both Pech de l'Aze and Devil's Tower 1 the temporomandibular (articular) tubercle is present, but the eminence itself is only weakly developed; it is not a continuous swelling across

the front of the fossa. The Pech de l'Aze glenoid fossa is less well developed than that of Devil's Tower 1. Alternatively, both La Quina 18 and Teshik Tash have very strong, continuous articular eminences. Both are comparable to the development of the >7-year-old modern humans used in this sample.

Collectively, cranial base and vault indicators support a developmental age comparable to that of a 4–6 year old modern human or Neandertal. The actual number of chronological years may vary considerably from this estimate, but the relative developmental stage suggests an individual in the later part of the early childhood years (*sensu* Bogin, 1988; Minugh-Purvis, 1988).

Adult cranial capacity

Reasonable cranial capacity estimates of the Mojokerto specimen range between 636 and 700 cc (Dubois, 1936; Jacob, 1966; Risçutia, 1975), with a direct liquid replacement measurement of 673 cc (Risçutia, 1975). Higher capacities have been suggested but seem unlikely (e.g. 730 cc [Weinert, 1938]). If Mojokerto's development is comparable to that of a 4–6-year-old modern human when 80–90% of cranial volume is attained (Scammon, 1930; Tanner, 1988), an adult cranial capacity of 740–860 cc would result, assuming *Hss* neural growth standards. Estimates of cranial capacity of adult Indonesian specimens, exclusive of Ngandong, range between 750 and 1,059 cc (Table 2) (Koenigswald, 1976; Holloway, 1981; Rightmire, 1993).

Cranial contours and superstructures

Adult *H. erectus* has a less rounded frontal and more angulated occipital than adult *H. sapiens sapiens* (Fig 4; Table 4). Slopes for frontal arc vs. chord are near one for *H. erectus* and slightly greater than one for *Hss*. However, *H. erectus* values are transposed significantly below those of *Hss*. Occipital slopes are near one for both species, but *H. erectus* y-intercept values ($y = 0.81$) are transposed significantly above *Hss* ($y = 0.08$). Parietal curvatures do not vary greatly between the species. Despite their larger cranial capacities, the Ngandong

hominids fall along the general trend of *H. erectus* for cranial curvatures.

Juvenile *H. sapiens sapiens* vault contours are neither more nor less rounded than their adult counterparts (Fig. 5; Table 4). However, juvenile *H. erectus* frontals (Ngandong 2, Skull III) and parietals (Skull III, KNM-WT 15000) are more rounded and their occipitals less rounded (KNM-WT 15000) than their adult counterparts. There are not enough data points to consider trends in the early *Homo* specimens.

Mojokerto has a more rounded frontal and parietal and less angulated occipital than adult Southeast Asian *H. erectus* (Fig. 4). Bivariate plots show the Ngandong 2 frontal is more rounded than the Ngandong adults (Fig. 4a). Ngandong 2 is in a similar if less extreme position relative to its adults as Mojokerto is relative to early adult Indonesian specimens (e.g., Trinil, Sangiran 2). The older juvenile/young adult Zhoukoudian Skull III has a slightly more rounded frontal than its adults, but its position is even less extreme than Ngandong 2. Mojokerto, KNM-WT 15000, and Skull III have more curved parietals than adult *H. erectus*. Both Mojokerto and KNM-WT 15000 have less angulated occipitals than their adult counterparts, whereas Skull III has an occipital that is as angulated as other adult Asian *H. erectus* (Fig. 4b).

Taxonomic affinity

Mojokerto possesses three features considered syn- or autapomorphic for *H. erectus*: an occipital torus, metopic eminence, and angulated occipital (Table 2; Figs. 1a, 2b). Although Mojokerto's occipital bone is not as highly angulated as in adult *H. erectus*, it shares a similar position as the juvenile KNM-WT 15000 relative to adult *H. erectus* (Fig. 4). Two syn- or autapomorphic characters are absent in Mojokerto: a sagittal keel and bregmatic eminence.

Mojokerto also possesses characters considered synapomorphic by some but not all researchers and characters that describe but do not define *H. erectus*. Mojokerto has a mastoid fissure and medial glenoid recess but lacks a sphenoid contribution to the glenoid fossa (Table 2). Of the characters of uncertain valence, Mojokerto possesses an

obelion depression (Fig. 1b,c), relatively strong postorbital constriction, and an incipient supratrochlear gutter (Fig. 2). Sagittal vault contours are similar to recognized *H. erectus* juveniles (Fig. 4). In addition, the Mojokerto temporomandibular joint (TMJ) is relatively broad anteroposteriorly, has a relatively strong articular eminence, and lacks a strong postglenoid process; all characters consistent with the *H. erectus* rather than the *H. habilis* (*sensu lato*) TMJ (Picq, 1990).

DISCUSSION

Despite limitations imposed by the preservation of the Mojokerto specimen, comparison with a large modern human growth series and juvenile fossil hominids suggests a developmental age range from 4–6 years rather than 1–8 years for the child. That is, the Mojokerto child died when in the later part of its early childhood years (*sensu* Bogin, 1988). This range precedes the human facial growth spurt, growth of cranial superstructures such as browridges, and eruption of the permanent dentition (Brodie, 1941; Minugh-Purvis, 1988).

Ontogeny of cranial vault contours

Growth of the cranial superstructures may result in differences in vault contours between adult *H. erectus* and *H. sapiens sapiens*. Cranial vault contours differ between adults of the two species and between juvenile and adult *H. erectus* but do not differ between juvenile and adult *Hss* (Figs. 4, 5). In short, juvenile *H. erectus* cranial contours are similar to those of both juvenile and adult modern humans (Fig. 5a). This suggests that growth of the secondary cranial structures (and the face) results in the differences in vault contours between adults of the two species. The similarity between adult human and juvenile *H. erectus* vault contours suggests that *Hss* is paedomorphic relative to *H. erectus* for vault shape (*sensu* Gould, 1977; Godfrey and Sutherland, 1996).

Differences in cranial size (volume) do not seem to produce differences in vault contours between *H. erectus* and *H. sapiens sapiens*. The Ngandong adults plot in the midst of other adult *H. erectus*, despite their larger cranial size (volume) (Fig. 4). Thus, *Hss* vault form is not merely the extension of

H. erectus growth patterns into hominids with larger brains. Differences between adults of the two species are likely to involve changes in the rate of growth or length of the growth period.

From a practical point of view, differences between adult and juvenile *H. erectus* vault contours provide one means of testing the relative developmental age of *H. erectus* adolescents as well as distinctions between adults and older adolescents. According to this criterion, Zhoukoudian Skull III is older than KNM-WT 15000 and may be a young adult; the Skull III occipital is adult in angulation, and the occipital and supraorbital tori are fully developed (Figs. 4, 5) (Black, 1931). This same technique in conjunction with an assessment of relative cranial development has shown that Sangiran 3 is a young adult (Antón and Franzen, 1996, in press). This technique may be useful for examining the various juvenile *H. erectus* recognized by Weidenreich (1941, 1943, 1951).

Mojokerto as Asian *H. erectus*

Despite Mojokerto's youth, the child exhibits three derived characters of *H. erectus*: an incipient metopic eminence, an angulated occipital, and an occipital torus. While not fully developed, the occipital torus's placement and form follow the pattern of all other *H. erectus*; it is a localized, horizontal thickening of the occipital squama that is most strongly developed at the midline and more attenuated laterally (Weidenreich, 1940c). The torus is similar in form and size to that of Zhoukoudian Skull VIII (Fig. 6 in Weidenreich, 1940c). The absence of the bregmatic eminence and sagittal keel in Mojokerto may be due to immature age rather than taxonomic status, as all of the cranial keels (metopic and bregmatic eminences, sagittal keel) and the occipital torus result from a localized thickening of ectocranial bone in *H. erectus* (Weidenreich, 1940c; Hublin, 1978, 1986). Since cortical and diploic bone are not fully differentiated until later childhood (>6 years), localized thickenings of the outer table may develop throughout the childhood years. Based on the Ngandong 2 frontal, the bregmatic eminence develops only after the metopic eminence is well established. We

might argue by extension that the sagittal keel also develops after the metopic eminence, although this cannot be confirmed on the basis of known juvenile *H. erectus* fossils.

Based principally on the synapomorphies Mojokerto possesses, augmented by shared characters of less certain valence (Table 2), Mojokerto is considered a juvenile *H. erectus*. Mojokerto's projected adult cranial capacity of between 740 and 860 cc is consistent with this designation. This designation agrees with that of Storm (1994), Weidenreich (1940a,b, unpublished), and Koenigswald (1936) but differs from Grimm (1940), Dubois (1936), and Koenigswald (1975) amongst others.

Mojokerto, the earliest Southeast Asian hominid, is not only *H. erectus* but also possesses characters considered by some to be autapomorphic for Asian *H. erectus* (e.g., cranial superstructures) (*sensu* Stringer, 1984; Wood, 1984). The earliest adult Asian *H. erectus*, Sangiran 27/31, also exhibits these Asian *H. erectus* autapomorphies at 1.6 mya (Crummett and Wolpoff, 1995). Although some researchers consider cranial keels plesiomorphic due to their presence in *Pan* and *Gorilla* (Kennedy, 1991) and *H. habilis* (Bräuer and Mbua, 1992) or not unique due to their presence in African *H. erectus* and *Hss* (e.g., Kennedy, 1991; Bräuer and Mbua, 1992), it is likely that the characters being scored are not homologous across these taxa (*sensu* Lieberman, 1995). For example, the structure of keeling in *Hss* from precontact California appears to be diploic, not tabular (ectocranial), in origin, unlike the condition in *H. erectus* (Antón, unpublished). That is, keeling in *H. erectus* may represent an autapomorphy related to the generalized cortical thickening of this species (*sensu* Kennedy, 1985; Hublin, 1986), whereas the presence of keeling across other taxa may be the result of homoplasy. Regardless of whether some African *H. erectus* also exhibit these characters, such characters are still more frequent in Asian than African *H. erectus* (Bräuer and Mbua, 1992) and may, in this sense, be considered regional characters.

Whether these regional characters are considered species specific (*sensu* Stringer,

1984; Wood, 1984; Tattersall, 1986; Howell, 1994) or geographic variants within a polytypic species (*sensu* Turner and Chamberlain, 1989), their presence in the earliest Southeast Asian hominids supports long-term morphological continuity within Asian *H. erectus*. Continuity (or replacement) within the early Southeast Asian hominid record does not, however, speak to the presence of continuity or replacement in the origins of modern humans in the region (contra Kramer, 1994). Support for either model of modern human origins must be based on morphological relationships between *H. erectus* and *Hss* and is not dictated by the finding of morphological continuity between earlier and later *H. erectus*. Although it has been argued that regional morphological links between *H. erectus* and *Hss* exist (e.g., Wolpoff et al., 1984; Wolpoff, 1996), other data suggest that characters used to link *H. erectus* to indigenous Australians are plesiomorphic because they are as prevalent in fossil African *Hss* from Afalou and Taforalt as in modern Australians (Lahr, 1994, 1996). A separate investigation concluded that many characters thought to link East Asian *Hss* and *H. erectus* are either primitive retentions or are not more prevalent in East Asian *Hss* than in other modern humans (Habgood, 1992). And other studies consider some of these characters plesiomorphies and still others homoplasies (Lieberman, 1995). Additionally, according to vault contour data presented here, the Ngandong specimens are no more like (i.e., transitional to) modern Australians than other *H. erectus*, despite their late age (Swisher et al., 1996) and despite the fact that the current *Hss* sample included fossil Australasians such as Kow Swamp 5 (Fig. 4; Table 1).

The early establishment and long continuity of the Asian *H. erectus* bauplan suggests that *H. erectus* characters may best be considered morphologically specialized/marginalized and perhaps even endemic to Asia (cf. Andrews, 1984; Howell, 1994). If the characters unique to *H. erectus* are indeed endemic to Asia/Southeast Asia, the validity of recognizing *H. erectus* in Africa is questioned. Recent work by Tattersall (1995) and Wood (1991, 1994) has suggested that much if not all of the African *H. erectus* hypodigm is

perhaps better considered *H. erectus*, although Wood still recognizes *H. erectus* at later time periods in Africa (e.g., OH-9). In this view it is the more generalized *H. ergaster* that gives rise to both *H. erectus* in Asia and *H. sapiens*. Alternatively, it has also been argued that the presence of these regional characters in the earliest adult Southeast Asian *H. erectus* is supportive of the center vs. edge model for regional evolution and does not therefore preclude the existence of a more generalized *H. erectus* in the center, Africa (Crummett and Wolpoff, 1995; Wolpoff, 1996). The current data cannot address either question directly. However, the early establishment and prolonged retention of *H. erectus* characters in Southeast Asia argues that these characters are indeed endemic to the region. I am inclined to view such endemism as suggestive that, at least the morpho-species, *H. erectus* is best viewed as an Asian/Southeast Asian phenomenon. If this is the case, Southeast Asian *H. erectus* may offer a situation analogous to Neandertals in Europe (*sensu* Hublin, 1990). If this is true, and *H. sapiens* later replaces *H. erectus* in Asia, we should expect to find late populations of *H. erectus* in Southeast Asia overlapping in time and space but not morphology with modern humans. New dates for Ngandong potentially provide such evidence (Swisher et al., 1996).

Whatever the wider interpretation, the comparison of Mojokerto with a large modern human growth series and juvenile fossil hominids has eliminated many of the discrepancies over developmental age and taxonomic status of the specimen. Systematic effort can produce taxonomically salient information from juvenile specimens.

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